Foraging Ecology of the Northern Goshawk in Coastal British Columbia

by

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Abstract

Effective wildlife conservation requires understanding diet composition and its consequences for population demography. I measured the diet of an at-risk population of Northern Goshawks (*Accipiter gentilis*) in southwestern British Columbia during two breeding seasons using pellets, prey remains, and nest cameras. I compared diet composition across two ecological zones and assessed the impact of dietary diversity and specialization on goshawk productivity. Goshawks consumed 33 different species but primarily consumed pine squirrels (*Tamiascuirus* spp.), which composed 14-61% of dietary biomass, depending on source. Diet composition differed slightly between the coastal and transition zones. I also conducted a pilot study of goshawk breeding season movement using GPS-UHF transmitters. Male goshawks used more space and travelled further from the nest than female goshawks. While I found no correlation between dietary diversity or specialization on pine squirrels and goshawk productivity, the abundance of this key prey species may affect goshawk productivity and space use.

Keywords: Northern Goshawk; *Accipiter gentilis*; diet; space use; breeding ecology; British Columbia

Dedication

This thesis is dedicated to itself.

> She developed an acute homesickness for Oxford and the *Study of Le Fanu*–a book which would never have any advertising value, but of which some scholar might some day moderately observe, “Miss Vane has handled her subject with insight and accuracy.”
>
> —Dorothy Sayers, *Gaudy Night*

To my thesis. I care.

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But in the end I am perhaps most grateful to you, dear reader. This work has taken more than two years of my life to complete, and I am pleased to think it may be of some use or interest to you. Thank you.

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Chapter 1

General Introduction

Once valued primarily for high timber yields, temperate rainforests of the Pacific Northwest are now managed with greater emphasis on the conservation of biodiversity (Thomas et al. 2006, Beese et al. 2019). One driver of this shift in management priorities is population declines in several species which rely on mature and old-growth forests. Some of these species have been placed under federal, provincial, or state protection: among others, the Marbled Murrelet (*Brachyramphus marmoratus*) is protected under the Species at Risk Act in Canada (COSEWIC 2014) and the coastal population of the pacific marten (*Martes caurina*) is protected under the Endangered Species Act in the United States (US Fish and Wildlife Service 2020). Management under these types of legislation is typically reactive and focused on conserving each imperiled species on a case-by-case basis (Simberloff 1998, Waples et al. 2013). The single-species approach has been widely criticized for failing to provide management for wider ecosystems, including the very ecosystems on which the imperiled species depend (Lambeck 1997, Waples et al. 2013). Alternatively, focusing on the broader scale of landscapes or entire ecosystems preserves the ecosystem processes and services on which wild species and humans alike depend (Franklin 1993, Pikitch et al. 2004). Yet ecosystem-based management is itself beset by numerous practical and theoretical challenges which have made it difficult to implement (Lambeck 1997, Simberloff 1998).

Managers have often turned to surrogate species as a solution for the dilemma posed by single-species and ecosystem-based management. At the core of the surrogate species concept is the belief that the needs or health of a single species, or a small suite of species, can stand in for the needs and health of numerous co-occurring species or ecosystem function (Caro 2010). Numerous variations and conflicting definitions are present in the literature, but the original concept may be that of the *indicator species*. The presence and population size of an indicator species is believed to reflect ecosystem processes or the

populations of other species (Landres et al. 1988). Perhaps more widespread than indicator species is the *umbrella species* concept. Protections which benefit umbrella species–typically wide-ranging habitat specialists–are assumed to confer protection to co-occurring species with smaller ranges and less restrictive habitat requirements (Roberge and Angelstam 2004, Seddon and Leech 2008). A related concept is the *flagship species*, a species whose protection, like an umbrella species, confers benefit on other species, but which is selected for its charisma and ability to serve as a rallying point for conservation (Andelman and Fagan 2000). These concepts all attempt to extend the relative simplicity of single-species methods to achieve the promise of ecosystem-based management (Lambeck 1997, Wiens et al. 2008).

No species better embodies the challenges of managing forest species and ecosystems in the Pacific Northwest than the Northern Spotted Owl (*Strix occidentalis caurina*, hereafter "spotted owl"). The spotted owl is strongly associated with old-growth temperate rainforests (Forsman et al. 2004) and has at various points been proposed as an indicator (Gutiérrez and Carey 1985), an umbrella (Tracy and Brussard 1994), and a flagship species (Simberloff 1998) for temperate rainforests in the Pacific Northwest. In the late 1980s, public outcry and litigation in the United States led to the development of a spotted owl conservation strategy concurrent with the species' listing as "threatened" under the Endangered Species Act (Thomas et al. 2006). This single-species plan rapidly expanded to include other species, particularly the Marbled Murrelet and several salmon stocks. The plan ultimately evolved into the Northwest Forest Plan, which currently governs federal lands in Washington, Oregon, and northern California. The Northwest Forest Plan remains rooted in spotted owl management, but also includes protections for watersheds, monitoring of rare species, and a sustainable annual timber harvest (Charnley 2006, DellaSala and Williams 2006). Not all the Northwest Forest Plan's goals have been achieved–notably, spotted owl and Marbled Murrelet populations have continued to decline, although at a slower rate–and some parts of the plan have been eroded under subsequent presidential administrations (DellaSala et al. 2015). Nonetheless, the Northwest Forest Plan remains a powerful example of an ecosystem-based management plan with a single species at its core.

The story of the Northern Goshawk (*Accipiter gentilis*, hereafter "goshawk") in North America parallels that of the Northern Spotted Owl. Two goshawk subspecies (*A. g. atricapillus* and *A. g. laingi*) are widely recognized and a third (*A. g. apache*) is acknowledged by some authors (Squires et al. 2020). The widespread *atricapillus* is found in boreal forests across the continent and ranges south into warmer pine-dominated forests in the west and mixed-deciduous forests in the east. The restricted *laingi* subspecies is smaller and sootier than *atricapillis* and found only along the west coast. The precise range of *laingi* is unclear; based on morphometrics, genetics, and ecosystem mapping, it is believed to extend along the west coast and islands of British Columbia, from Southeast Alaska to Washington's Olympic Peninsula (NGRT 2008, Sonsthagen et al. 2012, cf. Geraldes et al. 2018). The *apache* subspecies, while not widely accepted, is described as larger and darker-backed than *atricapillus*, and found in the high-elevation forests of the American Southwest (Squires et al. 2020). Goshawks are not associated with old-growth forest to the same degree as spotted owls, but do show a clear preference for breeding in extensive tracts of mature forest with large trees and dense canopies (Andersen et al. 2005, Squires and Kennedy 2006). As a wide-ranging predator associated with older forests the goshawk has, like the spotted owl, been proposed as a flagship (Sergio et al. 2006), an indicator (Hanley et al. 2005), and an umbrella species (Ozaki et al. 2006).

At the same time the Northwest Forest Plan was developing in the Pacific Northwest, alarms were sounded in the American Southwest over the impact of timber harvest on goshawks in arid montane forests (Crocker-Bedford 1990). Decades of litigation failed to list the southwestern goshawk population (proposed subspecies *apache*) under the Endangered Species Act, but a new management plan was eventually developed (Peck 2000). The single-species southwestern goshawk management plan disallowed timber harvest near known goshawk nests and required a minimum amount of mature forest be retained within the larger home range surrounding nests (Reynolds et al. 1992). Notably, the plan also specified the inclusion of younger forest, small clearings, snags, and woody debris to provide habitat for eight important goshawk prey species. This recommendation was based on the assumption that goshawks are habitat generalists limited by the abundance, not the availability, of prey–an assumption which has been the subject of heated debate (Greenwald et al. 2005, Reynolds et al. 2008). However, by incorporating

multiple species, dynamic ecosystem processes, and human use, the southwestern goshawk management plan approaches the principles of ecosystem-based management and shows its potential to scale up to a more cohesive plan in the style of the Northwest Forest Plan (Graham et al. 1994, Peck 2000).

In the temperate rainforests of the Pacific Northwest, naturalists described a small, dark subspecies of Northern Goshawk first found on the Haida Gwaii archipelago (Taverner 1940). The small size and sooty plumage of *A. g. laingi* may be an adaptation to the dark, dense forests the subspecies inhabits (Ethier 1999) and the agile avian prey believed to dominate its diet (McClaren et al. 2015, Penteriani et al. 2013). In the portion of its range within the United States the *laingi* subspecies has no additional protections, but in Canada it is designated as Threatened by COSEWIC (Committee on the Status of Endangered Wildlife in Canada; COSEWIC 2013). The *laingi* subspecies is further Red-listed by the British Columbia Conservation Data Centre and is an Identified Wildlife Species under the Forest and Range Practices Act (COSEWIC 2013).

The current management plan for *laingi* in British Columbia–the British Columbia Northern Goshawk Implementation Plan–emphasizes the protection of breeding habitat, particularly at small spatial scales around the nest. The plan focuses on the creation of breeding area reserves consisting of 200 hectares–a small portion of the estimated 3700-8500 hectare breeding season home range (Parks Canada Agency 2018)–of suitable breeding habitat surrounding known goshawk nests and their associated alternate nests (FLNRORD 2018). The identification of suitable breeding habitat is assisted by a habitat suitability index model developed using observed *laingi* nest site characteristics, information available in the literature, and expert knowledge (Mahon et al. 2008, NGRT 2008). A major long-term objective of the implementation plan is to include protection for the entire home range by expanding management to the larger foraging area which surrounds the breeding area (FLNRORD 2018). Some home ranges have already received protection beyond the breeding area through overlap with existing reserves, such as provincial parks or Old Growth Management Areas, or through the creation of Wildlife Habitat Areas. Management of the full home range under the implementation plan is similar to the goshawk management plan from the American Southwest, which also specifies protections for breeding habitat and foraging habitat at small scales and large scales around the nest,

respectively (Reynolds et al. 1992). However, unlike the plan from the American Southwest, the British Columbia Implementation Plan for *laingi* does not include management recommendations to increase the abundance or diversity of goshawk prey at any scale. In part this is due to the single-species nature of the plan, but it is also due to several knowledge gaps. While a habitat suitability index model does exist for goshawk foraging habitat in coastal British Columbia (Mahon et al. 2008), foraging ecology is poorly understood relative to breeding ecology. In particular, goshawk diet and prey communities in coastal British Columbia are not well studied (McClaren et al. 2015).

Ecosystem-based management has been implemented in some parts of coastal British Columbia, most notably in Haida Gwaii and the Great Bear Rainforest (Price et al. 2009, Takeda and Røpke 2010), where the Northern Goshawk has been incorporated as a focal species. Goshawk managers have acknowledged a landscape-scale plan would be an improvement over the practice of managing at the scale of individual nests (NGRT 2008). Together these suggest an ecosystem-based approach incorporating the Northern Goshawk as a focal species may be possible for coastal rainforests throughout in British Columbia. However, the knowledge gaps surrounding goshawk foraging ecology hinder current single-species and potential ecosystem-based management alike.

My thesis sets out to fill one knowledge gap identified by the Northern Goshawk Recovery Team (NGRT) by providing basic ecological information regarding the breeding season diet of goshawks in coastal British Columbia (NGRT 2008). The following chapter describes my research quantifying goshawk diet in coastal British Columbia with a focus on potential dietary variation at the broad ecosystem scale, and investigating potential links between dietary variation and goshawk reproductive success. The final chapter summarizes my results, describes the outcome of a pilot study of goshawk space-use, and discusses the implications of both for management and future research efforts.

Chapter 2

Northern Goshawk Diet in the South Coast of British Columbia

2.1 Introduction

Effective wildlife conservation often requires understanding diet composition and its consequences for population demographics (Ferrer and Negro 2004, Stier et al. 2016). Specialist predators consume a narrow range of prey species, which increases foraging efficiency on preferred prey at the cost of decreased reproductive success for the specialist when that prey is scarce (Newton 1998). Generalist predators consume a greater diversity of prey and readily switch between prey species, so are less sensitive to changes in prey abundance (Steenhof and Kochert 1988, Terraube and Arroyo 2011). However, for a generalist predator a single key prey species may still be a major driver of reproductive success (Elmhagen et al. 2000, Resano-Mayor et al. 2016). For at-risk predators, increasing the abundance of key prey species may consequentially be a useful conservation tool (Ferrer and Negro 2004, Forsman et al. 2004, Resano-Mayor et al. 2016).

The northern goshawk (*Accipiter gentilis*) is a large forest-dwelling raptor with a Holarctic distribution. A generalist predator, the goshawk hunts a variety of small- and medium-sized mammals and birds, including squirrels, rabbits and hares, grouse, jays and crows, and pigeons (Squires et al. 2020). Despite this diverse diet, a single prey species or narrow suite of species has a strong effect on the demographics of many goshawk populations. In the Yukon, goshawks depend on snowshoe hare (*Lepus americanus*) and show strong variation in productivity, mortality, and space use in response to cyclical changes in hare abundance (Doyle and Smith 1994). Goshawks in Scandinavia likewise rely on a single prey taxon and show changes in productivity and occupancy based on the annual abundance of four grouse species (subfamily Tetraoninae; Tornberg et al. 2005). In contrast, goshawks in the American Southwest have a wide prey base and regularly consume some fourteen different

species (Boal and Mannan 1994). Fluctuations in goshawk productivity in this region are small and driven by total prey abundance, though the most influential single prey species is red squirrel (*Tamiasciurus hudsonicus*) (Salafsky et al. 2007). These examples suggest the identity and influence of key prey species in such an adaptable predator may be specific to each population and its respective ecosystem.

In British Columbia, Canada, the coastal population of Northern Goshawks is the subject of federal and provincial management which focuses on the protection of breeding habitat and the increase of nest site availability (COSEWIC 2013, FLNRORD 2018, Parks Canada Agency 2018). Like many raptors, goshawks are generally considered to be limited by both nest site availability and prey abundance (Reynolds et al. 2006, Rutz et al. 2006). However, current management plans contain minimal protections for foraging habitat and do not include actions to increase prey populations, in part due to a lack of knowledge regarding goshawk diet and foraging behavior in coastal British Columbia (FLNRORD 2018, Parks Canada Agency 2018).

Goshawk diet across the wider coastal Pacific Northwest is variable. Goshawks on Vancouver Island, British Columbia, consume primarily red squirrels (Ethier 1999) whereas goshawks in nearby southeast Alaska (Lewis et al. 2006) and western Washington (Bloxton 2002) consume mostly medium and large birds. Even within coastal British Columbia differences between island and mainland communities, combined with a variation in temperature and precipitation, produce a gradient of forest types which support a range of goshawk prey assemblages. For example, snowshoe hare, a key prey species in many portions of the goshawk's range, is absent from Vancouver Island, scarce on the coastal mainland, and abundant in the British Columbia interior (Nagorsen 2005). Goshawk diet in coastal British Columbia may reflect this variation in available prey between Vancouver Island and the mainland, as well as the variation in prey abundance between the coast and the interior. Where coastal forest types transition to interior forest types, it is unclear how goshawk diet responds to fine variation in prey availability and abundance.

Here we describe the breeding season diet of northern goshawks in the south coast of British Columbia over a two-year period using nest cameras, egested pellets, and prey remains. We assess whether goshawk diet at the nest differs within the south coast region

between the wetter *coastal ecosystem zone* and the drier *transitional ecosystem zone*. We further evaluate whether diet composition and diet diversity influence goshawk reproductive success.

2.2 Methods

2.2.1 Study Area and Species

In North America the northern goshawk ranges from the boreal forests of the Yukon south to the high-elevation forests of Arizona and New Mexico. Two subspecies are recognized: the widespread *atricapillus* and the restricted *laingi* (Squires et al. 2020). The *laingi* subspecies was first described on the Haida Gwaii archipelago in British Columbia and is smaller and darker than the *atricapillus* subspecies found elsewhere on the continent (Taverner 1940). The subspecies' range is limited to the west coast of North America, from southeast Alaska through mainland British Columbia and Vancouver Island, and possibly as far south as Washington's Olympic Peninsula (COSEWIC 2013). Within British Columbia, the Coast Mountains form a major barrier to movement and mark the boundary between the *laingi* subspecies found on the coast and the *atricapillus* subspecies found in the interior. *A. g. laingi* is considered a species at risk in British Columbia by both the federal and provincial governments due to significant habitat loss from industrial timber harvest (NGRT 2008, COSEWIC 2013).

We conducted research in the south coast of British Columbia, where goshawks are considered part of the *laingi* subspecies (NGRT 2008, COSEWIC 2013, but see Geraldes et al. 2018). The region is characterized by rugged mountains interspersed with coastal fjords and low-lying valleys. The maritime climate supports temperate rainforest dominated by western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and Douglas-fir (*Pseudotsuga menziesii*; Meidinger and Pojar 1991). Within the south coast of British Columbia, goshawk managers have delineated a *transitional ecosystem zone* (hereafter "transition zone") composed of low-elevation valleys in the Coast Mountain Range which connect the *coastal ecosystem zone* (hereafter "coast zone") and the interior (NGRT 2008). The coast and transition zone are defined using a biogeoclimatic (BEC) zone classification system which incorporates climate, physiography, and climax vegetation characteristics (Meidinger and Pojar 1991).The coast zone follows the boundaries of the Coastal Western

Hemlock (CWH) zone and its variants on the mainland coast of British Columbia, excepting the drier zonal variants (CWH dry submaritime, CWH moist submaritime, CWH wet submaritime) which make up the transition zone (NGRT 2008). The temperate rainforest ecosystems of the narrow transition zone are slightly drier than the forests found further west in the coastal zone and somewhat intermediate with the arid interior forests found further east (Fig. 2.1). The transition zone may represent an area of overlap between the coastal *laingi* population and the interior *atricapillus* population (NGRT 2008).

2.2.2 Data Collection

We assessed goshawk diet during the 2019 and 2020 breeding seasons through a combination of egested pellets, prey remains, and nest camera photos. Active goshawk nests were located as part of long-term population surveys conducted by the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development (FLNRORD). For detailed survey methodology see McClaren (2005). Some study sites contained active nests in both years of the study.

We collected prey remains and egested pellets from 33 nests at 24 sites (2019 n = 18 nests, 2020 n = 15 nests, sites with nests in both years n = 9). We gathered pellets and remains from beneath active nests, from within nests after juveniles fledged, and from plucking-posts located within the site. Logistic constraints prevented more than one collection of pellets and remains at most sites, but we visited some sites multiple times during the breeding season. All prey remains and all pellets from a collection location (one nest or one plucking post) were combined into a single sample for each visit to that location. The sample size of pellets and remains for each nest varied based on number of surveyor visits, duration of surveyor search, and weather conditions preceding surveyor visit.

We installed nest cameras at a subset of 14 of these nests in 12 sites (2019 n = 6 nests, 2020 n = 8 nests, sites with nests in both years n = 2) to record prey delivered to the nest. Nest cameras are an effective and relatively unbiased method of measuring avian diet (García-Salgado et al. 2015, Harrison et al. 2019). However, cameras may overestimate prey deliveries because goshawks cache prey items for redelivery to the nest at a later time, which creates a risk of double-counting items. Due to the discrete nature of our data

we were unable to differentiate cached, re-delivered items from new items and did not attempt to account for caching in our analysis. Previous nest camera-based studies of goshawk diet have observed low numbers of cached items (Smithers et al. 2005: 8.3%, Lewis et al. 2006: 7.3%). Although we acknowledge caching is a potential source of bias, based on these numbers we do not believe our failure to account for it will substantially alter our results. We also did not attempt to differentiate between prey consumed by the female at the nest and prey consumed by the chicks.

Nest cameras were digital trail cameras (Reconyx brand, UltraFire and HyperFire models) mounted 2-5 meters distant from and slightly above the nest, usually in an adjacent tree. Cameras in 2019 were programmed to take three photos one second apart when triggered by motion and an additional one photo every thirty minutes. Cameras in 2020 were programmed to take five photos one second apart when triggered by motion and an additional one photo every twenty minutes. Installation took place during the early nestling phase (between 4 June and 18 July; mean installation date 7 June) and cameras were left in place until late fall or early winter, after juveniles had dispersed. Camera site selection was not random but constrained by topography, site access, and timing of nest discovery. We observed no nest abandonment following camera installation.

Breeding chronology was not available for most sites. At 12 of the 14 nests with cameras (2019 n = 6, 2020 n = 6, sites with nests in both years n = 1), we aged chicks using a pictorial guide (Boal 1994) from photos taken shortly after camera installation. We defined productivity as the number of chicks to reach 32 days of age (Boal 1994, McClaren et al. 2002).

2.2.3 Diet Quantification

We reconstructed prey from pellets and prey remains following a modification of the protocol used by Lewis et al. (2004). Within each sample, we identified remains to the lowest possible taxonomic category and counted the minimum number of individuals (i.e. 3 hare femurs = 2 *Lepus americanus*). Intact pellets and broken but reassembled pellets were analyzed individually within each sample, while fragmented pellets were combined within each sample. We dissected pellets and identified feathers, fur, and hard parts to the lowest taxonomic level possible. We counted the minimum number of individuals represented

within the pellet or pellet collection. Additionally, we categorized prey items from pellets and remains by size (small = sparrow- or vole-sized, medium = jay- or squirrel-sized, and large = grouse- or hare-sized).

We assigned mass to prey items identified to species using data from the literature. We assigned mass to mammals from Nagorsen (2002) and to birds from Billerman et al. (2020), using the geographically closest estimates available and averaging the mass of males and females. We treated some homogenous genera for which we could not differentiate species (such as *Eutamias* and *Myotis*) as a single taxonomic grouping. For these genera, we assigned mass by averaging the masses of all possible species, based on range maps. Red squirrels (*Tamiasciurus hudsonicus*) were present at a single site within our study area; when unable to distinguish between the two members of the genus *Tamiasciurus* we assigned the item to the more common *T. douglasii*. Unidentified grouse were common among remains; we assigned these the mean mass of the two grouse species present in our study area (*Bonasa umbellus* and *Dendragapus fulignosus*). We assigned juvenile prey items (primarily grouse) 50% of the adult mass. We assigned prey mass for unidentified items by averaging the masses of the identified species in that size category and taxonomic class (Table 2.1).

Data from prey remains and egested pellets are known to be biased indices of diet (Tornberg and Reif 2007, Simmons et al. 1991). Some authors have found combining data from both sources to produce relatively unbiased results that can serve as a helpful supplement to nest camera data (Lewis et al. 2004, Simmons et al. 1991). A preliminary examination of differences between pooled pellets-and-remains data and camera data indicated large differences between these two sources. We therefore report results from pellets, pooled pellets-and-remains, and cameras separately. We do not report results from prey remains alone.

We reviewed nest camera photos and identified each new prey item delivered to the nest to species when possible. When items could not be identified to species, we identified them to the lowest possible taxonomic level. We assigned prey items identified from photos a size category and biomass by the same method used for remains and pellets. We assigned partial items the average mass for that size category and taxonomic class.

We quantified goshawk diet across the entire study area in several ways using data from pellets, pooled pellets-and-remains, and nest cameras. For ease of comparison, we grouped prey items into eight broad categories based on taxonomy, frequency of occurrence, and predicted importance in the diet based on previous goshawk diet studies: pine squirrels (genus *Tamiasciurus*), hares (genus *Lepus*), all other mammals, grouse (subfamily Tetraoninae), thrushes (family Turdidae), corvids (family Corvidae), all other birds, and unidentified items. We calculated the percent biomass of each group, as well as the percent biomass of all avian and all mammalian items. For nests with cameras, we additionally quantified diet at the level of the individual nest and further calculated diet diversity with Simpson's Diversity Index (Simpson 1949) using counts of items identified to genus or better. We report diet as the percent of biomass or the mean percent biomass $\pm$ the standard deviation, except where counts of items or percent of items are explicitly specified.

2.2.4 Statistical Analysis

We classified sites as either coastal or transition based on whether the site was centered within the transition zone defined by NGRT (2008). We used counts of items assigned to the eight broad prey categories to assess differences in goshawk diet between the coastal and transition zones. We combined all data within each zone and tested each data source separately for disproportionate use of prey in each category between zone and source using a chi-squared test with simulated Monte Carlo *p*-values (2000 permutations) due to small sample sizes (Hope 1968). For nests with cameras, we also calculated the percent *Tamiasciurus* spp. (hereafter "pine squirrel") biomass, which is known to be an important food source for goshawks in British Columbia (Ethier 1999), and diet diversity at the individual nest level and compared these between the zones using a *t*-test. Finally, we tested for differences in goshawk productivity between the two zones using a *t*-test.

To determine the potential reproductive consequences of dietary variation, we examined how two aspects of diet, diet diversity and the percent squirrel biomass in the diet, influenced productivity using simple linear regressions. We pooled data from both years of the study after testing for differences in prey group composition (combining all data within each year and source and applying a chi-square test), diet diversity (using a *t*-test of nest

camera data), proportion squirrel biomass (using a *t*-test of nest camera data), and productivity (using a *t*-test of nest camera data) between years and finding no significant differences. We tested for dietary differences between years using all data sources, but because productivity data were available only from sites with nest cameras and nest-level diet data from pellets and prey remains were sparse, we performed this analysis using only diet data from nest cameras. We included all available nests with productivity data in this analysis, including one site which contained an active nest in both years of the study. Averaging variables for this site across years or including a single randomly selected year does not alter the presented results. All analyses were performed in R version 4.0 (R Core Team 2020). We used a significance level of $P = 0.05$ for all tests.

2.3 Results

2.3.1 Goshawk Diet

We identified a total of 9 unique species from pellets collected at 25 nests. No pellets were collected from 8 sites. Of the 135 prey items obtained from pellets, we identified 58% to genus or better and identified all items at least to class. Of the 121 prey items obtained from remains, we identified 51% to genus or better and identified all items at least to class. We identified 17 species from remains collected at 30 nests, for a total of 20 unique prey species from the pooled pellets-and-remains sample (Table 2.2). No remains were collected from 3 sites.

The majority of prey identified from pellets were mammalian (75% of biomass). Pine squirrels made up 61% of biomass, while other birds (neither grouse, corvids, nor thrushes) made up 21% and other mammals (neither pine squirrels nor hares) made up another 14%. Corvids and thrushes made up the remaining 4% of biomass. No hare or grouse were identified from pellets.

In contrast, the majority of prey identified from the pooled pellets-and-remains sample were avian (64% of biomass). The largest prey group was grouse (36%), followed by other birds (24%) and hare (18%). Pine squirrels made up only 14% of the pooled sample and other mammals made up another 5%. The remaining 3% of biomass was made up of corvids and thrushes.

We identified a total of 25 unique species from 566 prey deliveries recorded on 14 nest cameras (Table 2.2). After excluding 69 deliveries which were completely obscured from the cameras, each nest contributed an average of 36 items (range 1 - 69). We were able to identify 60% to genus or better and 77% at least to class. Small and medium birds were disproportionately represented among items identified only to class, frequently arriving at the nest already plucked and decapitated. Variability in the number of items recorded and the rate of identification was due to differences in camera placement and sensitivity settings.

The majority of prey identified on nest cameras were mammalian (71% of biomass, $\bar{x}$ = 69 $\pm$ 12, *n* = 14). Birds accounted for only 18% of biomass ($\bar{x}$ = 18 $\pm$ 12), and the remaining 11% could not be identified to class ($\bar{x}$ = 19 $\pm$ 26). The high proportion of mammalian biomass was driven by the dominance of pine squirrels (47% of biomass, $\bar{x}$ = 49 $\pm$ 14) and other mammals (17%, $\bar{x}$ = 17 $\pm$ 12). Unidentified items accounted for 11% of biomass ($\bar{x}$ = 19 $\pm$ 26). The remaining biomass was composed of hare (8%, $\bar{x}$ = 31 $\pm$ 2), other birds (9%, $\bar{x}$ = 10 $\pm$ 10), grouse (5%, $\bar{x}$ = 9 $\pm$ 5), thrushes (3% , $\bar{x}$ = 3 $\pm$ 3) and corvids (1%, $\bar{x}$ = 3 $\pm$ 3). Overall diet diversity for the study area, based on counts of items identified to genus or better, was moderate (0.57). Diet diversity of individual nests was highly variable, ranging from 0 to 0.72 ($\bar{x}$ = 0.47 $\pm$ 0.21).

2.3.2 Difference in Northern Goshawk Diet Between Ecological Zones

We observed a difference in the diet of goshawks in the coastal and transition zones (Table 2.3), although these differences were more pronounced in the pooled pellets-and-remains data (χ^2 = 19.18, *P* = 0.003) and camera data (χ^2 = 21.52, *P* = 0.005) than in data from pellets alone (χ^2 = 7.53, *P* = 0.11; Fig. 2.2). A post-hoc test incorporating a Bonferroni correction for multiple comparisons (adjusted α = 0.007) revealed the difference between zones observed in the pooled pellet-and-remains data was driven by the number of other birds and hares. Other birds were observed significantly more often in the diet of goshawks in the coastal zone (χ^2 = 12.6, *P* = 0.002), whereas hare were observed significantly more often in the diet of goshawks in the transition zone (χ^2 = 7.22, *P* = 0.01). Similarly, a post-hoc test of the camera data (adjusted α = 0.006) found the difference between zones

to be due to the significantly higher frequency of unidentified prey items in the coastal zone relative to the transition zone (χ^2 = 15.37, *P* = 0.001).

We observed no significant difference in diet diversity (study area $\bar{x}$ = 0.47 $\pm$ 0.21; coastal zone $\bar{x}$ = 0.29 $\pm$ 0.24, *n* = 5, transition zone $\bar{x}$ = 0.55 $\pm$ 0.14, *n* = 9; *t* = -2, df = 3.92, *P* = 0.12) or the proportion of squirrel biomass (study area $\bar{x}$ = 49 $\pm$ 14; coastal zone $\bar{x}$ = 57 $\pm$ 20, *n* = 5, transition zone $\bar{x}$ = 45 $\pm$ 10, *n* = 9; *t* = 1.19, df = 3.79, *P* = 0.3) between the zones when using individual nest-level data from nest cameras.

2.3.3 Productivity

We were able to measure productivity (the number of chicks to reach 32 days of age) for 12 of 14 nests monitored with nest cameras. We were not able to obtain productivity data from two nests because the camera memory cards filled prior to fledging.

Goshawks successfully fledged young from 11 of 12 nests with productivity data available, producing 0-3 chicks per active nest ($\bar{x}$ = 1.36 $\pm$ 0.81) and 1-3 chicks per successful nest ($\bar{x}$ = 1.55 $\pm$ 0.69). Siblicide was common, accounting for two of the three deaths in the failed nest and one death in each of four other nests. We observed no difference in productivity between years ($\bar{x}$ = 1.42 $\pm$ 0.79; 2019 $\bar{x}$ = 1.67 $\pm$ 1.03, *n* = 6; 2020 $\bar{x}$ = 1.17 $\pm$ 0.41, *n* = 6; *t* = 1.1, df = 6.53, *P* = 0.31). Nor did we observe any difference in the prey group composition between years (using counts of items) in either data from nest cameras (χ^2 = 5.27, *P* = 0.65), pooled pellets-and-remains (χ^2 = 1.46, *P* = 0.85), or pellets alone (χ^2 = 0.4, *P* = 0.99). We also observed no difference in diet diversity ($\bar{x}$ = 0.47 $\pm$ 0.21; 2019 $\bar{x}$ = 0.56 $\pm$ 0.16; 2020 $\bar{x}$ = 0.4 $\pm$ 0.22; *t* = 1.49, df = 10.82, *P* = 0.17) or proportion of squirrel biomass ($\bar{x}$ = 49 $\pm$ 14; 2019 $\bar{x}$ = 44.57 $\pm$ 9.88; 2020 $\bar{x}$ = 45.89 $\pm$ 24.43; *t* = -0.14, df = 9.74, *P* = 0.89) between years.

We found little evidence to suggest goshawk productivity was influenced by either the proportion of diet composed of pine squirrel biomass (F_1 = 0.72, df = 9, *P* = 0.42) or diet diversity (F_1 = 1.31, df = 9, *P* = 0.28; Fig. 2.3). There was also no significant difference in goshawk productivity between the coastal and transition zones (*t* = 0.93, df = 4.71, *P* = 0.4).

2.4 Discussion

Goshawk survival, migration, reproductive success, and other demographic parameters are often related to the abundance of a key prey species (Doyle and Smith 1994, Tornberg et al. 2005, Rutz and Bijlsma 2006). Although we lacked data on prey abundance within our study area, other authors have found goshawk diet reflects site-level prey abundance (Rogers et al. 2006, Lewis et al. 2006). We observed significant variation in the proportion of pine squirrel biomass delivered to each nest, which may mirror differences in squirrel abundance between sites. However, we did not find evidence to support an effect of this variation on goshawk productivity. When key prey abundance is low, high diet diversity may indicate a reliance on alternate prey, with associated negative reproductive consequences (Resano-Mayor et al. 2016). We found no evidence of an effect of diet diversity on goshawk productivity but, notably, the only nest in our study to experience a complete breeding failure received the smallest percent squirrel biomass we observed. Given the strength of evidence from other studies and the clear importance of pine squirrels in the diet of this population, it seems probable pine squirrel abundance has some effect on goshawk productivity. Tree squirrels experience large fluctuations in abundance following cyclical changes in conifer seed crop size (Smith 1970). Given the potential cascading consequences for goshawks, understanding the relationship between variation in pine squirrel abundance and goshawk demography remains a crucial knowledge gap.

Across much of North America the key goshawk prey species is usually mammalian, often from the family Leporidae or Sciuridae (Table 2.4; Boal and Mannan 1994, Doyle and Smith 1994, DeStefano et al. 2006, Rogers et al. 2006, Miller et al. 2014). However, in the coastal temperate rainforests of the Pacific Northwest, goshawk diet generally contains more birds than mammals and the key prey is usually a species of grouse (subfamily Tetraoninae; Watson et al. 1998, Thrailkill et al. 2000, Bloxton 2002, Lewis et al. 2006). Despite inhabiting coastal rainforests, goshawks on Vancouver Island, British Columbia, consume primarily red squirrels (*T. hudsonicus*; Ethier 1999). Our results from the coastal mainland of British Columbia are consistent with findings from Vancouver Island and more broadly with results from the interior of North America but stand in contrast to findings from elsewhere in the Pacific Northwest. Goshawk diet varies at large scales in response to available prey species and prey abundance (Drennan 2006), suggesting pine squirrel abundance is higher

within Vancouver Island and the south coast than other temperate rainforest ecosystems.

Prey availability and abundance may also vary at fine scales due to differences in habitat type (Kenward 1982, Penteriani et al. 2013). Within our study area, low-elevation mountain valleys bridge the wet forests of the coast and the dry forests of the interior, creating a narrow region of intermediate habitat types (NGRT 2008). Coastal rainforests are believed to contain a lower overall abundance of goshawk prey (McClaren et al. 2015) and a lower abundance of key mammalian prey, such as snowshoe hare (Nagorsen 2005), than interior forests. Available prey species and prey abundance in the transition zone may be intermediate between the coastal zone and the interior, with associated consequences for goshawk diet and demography. We found mixed evidence for a difference in goshawk diet between the two zones. Overall, our analyses show the diet of goshawks in the transition zone is very similar to that of goshawks in the coastal zone. However, data from pooled pellets-and-remains indicate goshawks in the coastal zone consume more small- and medium-sized birds than goshawks in the transition zone, consistent with the hypothesis that the coastal zone is relatively depauperate of mammalian prey. Identifying small and medium birds was more difficult using nest cameras than for other data sources. The high number of unidentified prey items recorded on coastal zone cameras may be further evidence goshawk diet there contains relatively more avian prey than in the transition zone. Given our small sample size and the large variation in diet between nests it is difficult to make any strong conclusions regarding dietary variation between the zones. However, any dietary difference between the coastal and transition zone appears to be minor and the importance of pine squirrels appears to be universal.

Raptor diet is studied through a variety of indirect methods, such as the collection of pellets and prey remains, and direct methods, such as nest cameras and observation from blinds. Nest cameras are considered one of the least biased methods for measuring diet at the nest in raptors (Tornberg and Reif 2007, García-Salgado et al. 2015, Harrison et al. 2019). Cameras in this study provided significantly more data at a finer resolution than either pellets or prey remains, which could only be collected during the infrequent surveys each site received. However, the cost, effort, and logistical challenges of camera installation restricted the number of sites from which camera data could be collected. Additionally,

technical issues relating to camera settings and placement resulted in a loss of data at some sites. Despite these limitations, we believe nest cameras provided the most accurate and complete picture of goshawk diet. Compared to cameras, pellets were relatively unbiased in measuring coarse diet composition, but severely underestimated prey species richness. The pooled pellets-and-remains sample captured a much greater prey richness, including several species not detected on nest cameras, but greatly overestimated the proportion of avian biomass relative to camera data. Measuring diet composition by counts or biomass adds further uncertainty, with measurements of counts overestimating avian prey relative to measurements of biomass. These complex results highlight the importance of clearly reporting the source and measurement of raptor diet data. Because these methods have all been used in past studies we believe there is value in reporting the results of each for ease of comparison. However, we advocate for future diet studies to prioritize collecting data via cameras, either video or still images, rather than physical specimens.

Our study addresses a fundamental question regarding the basic ecology of an at-risk population of the northern goshawk. This population is currently considered part of *A. g. laingi*, a subspecies restricted to the coastal Pacific Northwest. In portions of *laingi*'s range the diet is dominated by mammalian prey, specifically pine squirrels (this study, Ethier 1999), and in others by avian prey (Bloxton 2002, Lewis et al. 2006). Pine squirrels clearly play a key role in the diet of some *laingi* populations, including the population of Haida Gwaii (Roberts 1997, cited in COSEWIC 2013), where red squirrel is an introduced species. Genetic evidence indicates goshawks on this isolated archipelago may be distinct from goshawks on the mainland coast and Vancouver Island (Sonsthagen et al. 2012, cf. Geraldes et al. 2018). Regardless of their taxonomic relationship, dietary evidence suggests the goshawk populations of Haida Gwaii, Vancouver Island, and the mainland coast are more similar to each other in foraging habits and habitats than to other putative *laingi* populations. Ecological similarity, such as diet and habitat characteristics, may therefore prove a better guide than genetic similarity when incorporating foraging habitat protection or prey population management into conservation plans.

2.5 Figures and Tables

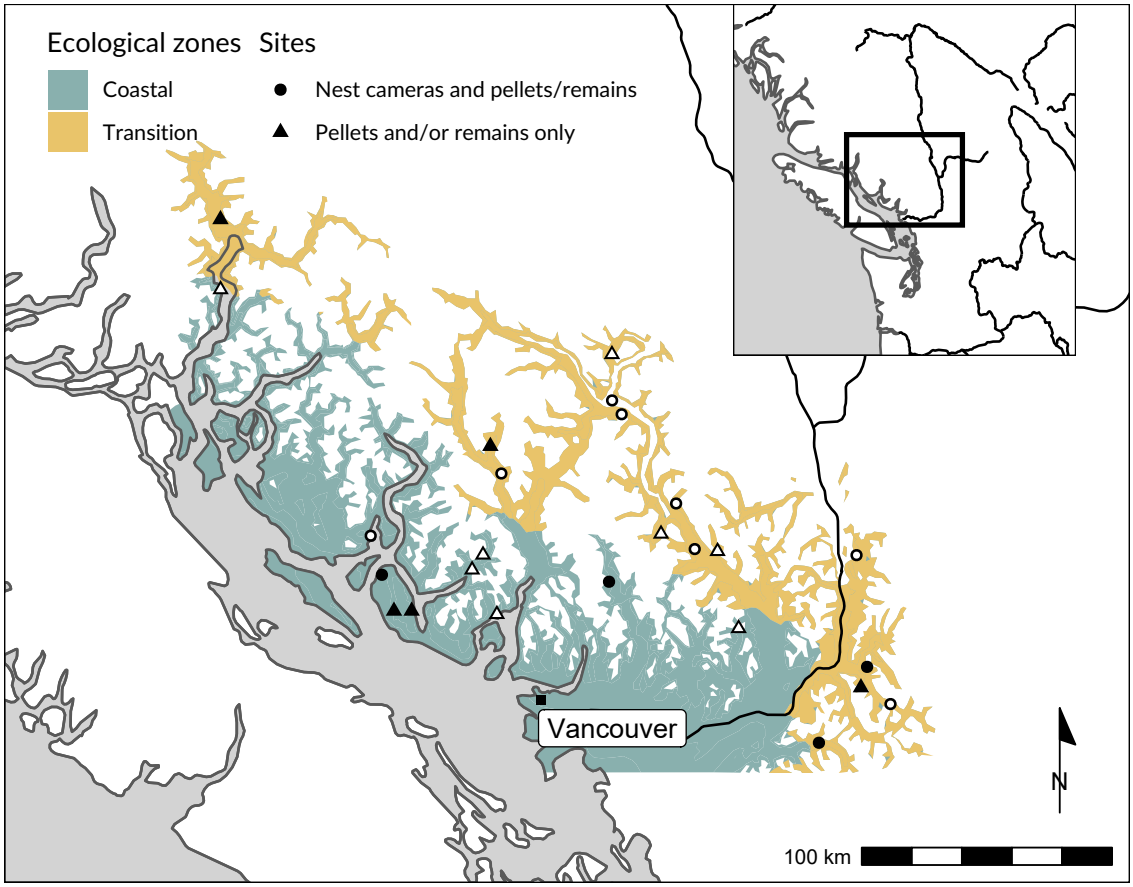

Figure 2.1: Map of the south coast of British Columbia showing the coastal (green) and transition (gold) zones as well as sites where nest cameras photos, egested pellets, and prey remains were collected (circles) and sites where only pellets and/or remains were collected (triangles). Sites with one year of data are shown with open symbols and sites with two years of data with closed symbols.

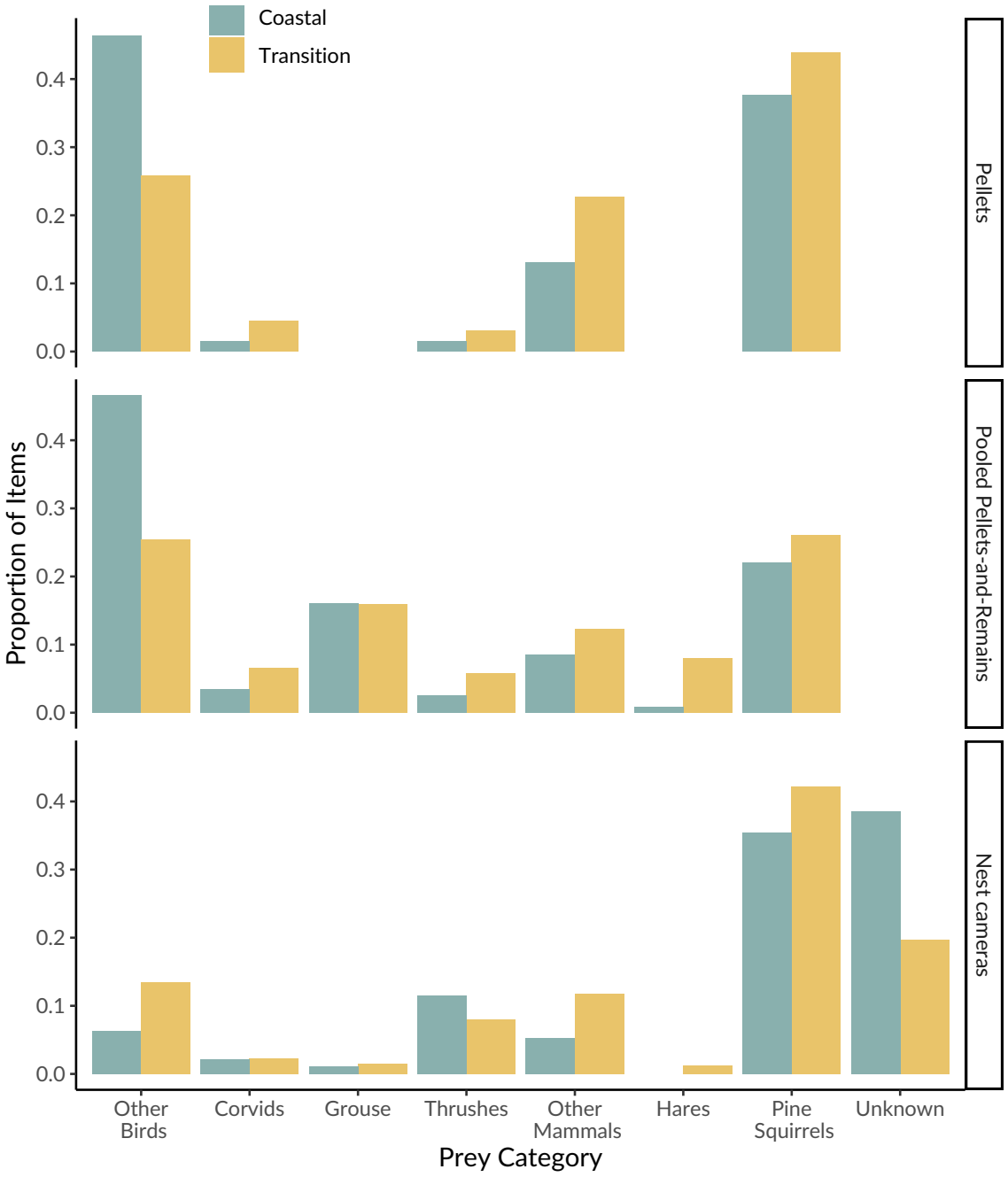

Figure 2.2: Diet composition of Northern Goshawks from the coastal (green) and transition (gold) zones of south coast British Columbia estimated using nest cameras, pellets, and pooled pellets-and-remains. Prey categories include three major avian taxa with other birds pooled, two major mammalian taxa with other mammals pooled, and an unknown category containing unidentified items.

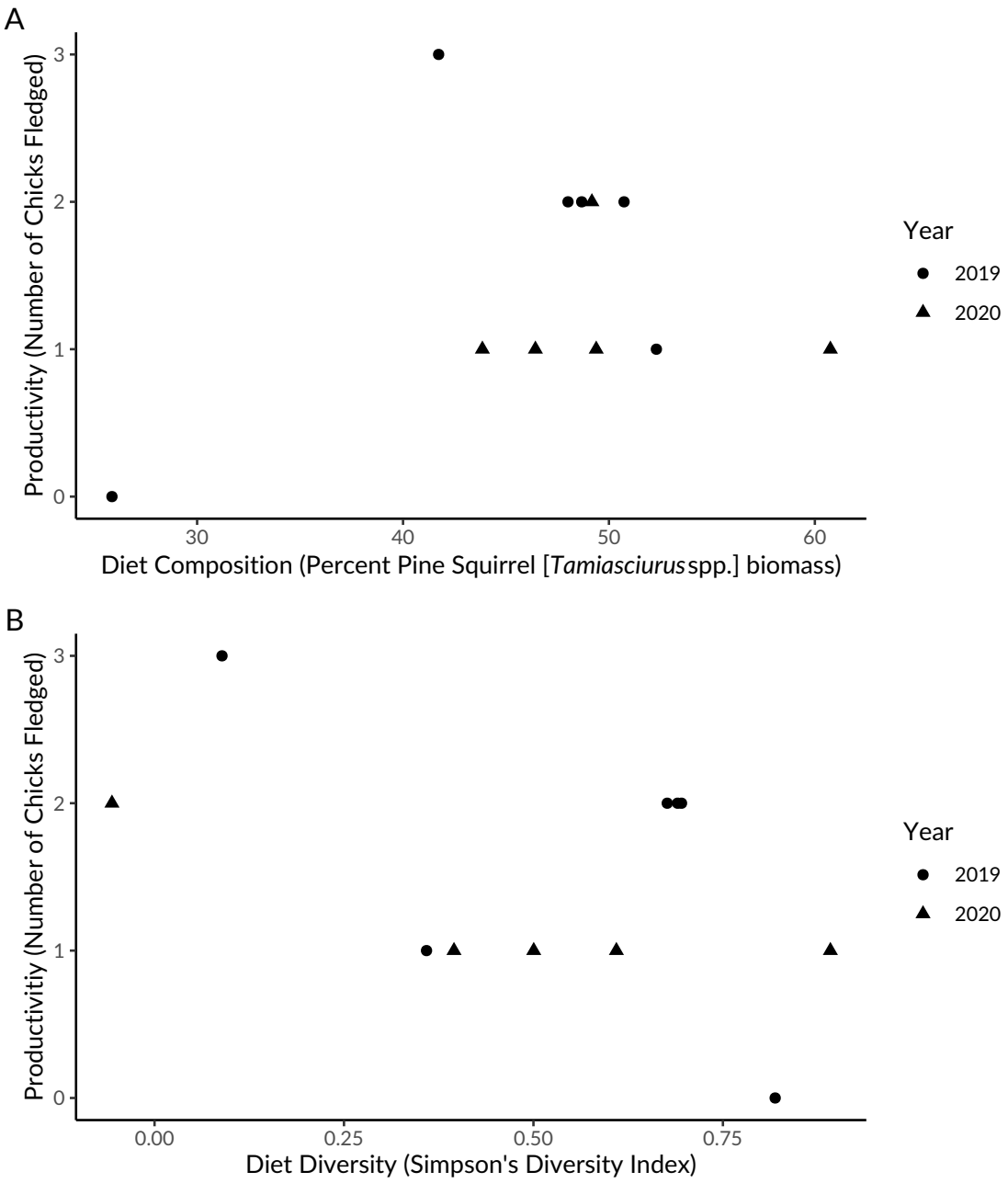

Figure 2.3: Relationship of diet composition (A) and diet diversity (B) to the productivity of Northern Goshawks at 12 sites in south coast British Columbia in 2019 and 2020.

Table 2.1: Mass of identified prey species and estimated mass of unidentified prey items, categorized by size and class, used to calculate the proportional biomass in the diet of Northern Goshawks in south coast British Columbia. Mass estimates taken from Billerman et al. 2020 and Nagorsen 2002. Mean of both sexes used for sexually dimorphic species.

Prey type		Mass (g)
Large Bird		
Northern Goshawk	*Accipiter gentilis*	857.2
Mallard	*Anas platyrhynchos*	1138.5
Duck	*Anas* sp.	867.3
Ruffed Grouse	*Bonasa umbellus*	523.4
Great Horned Owl	*Bubo virginianus*	1505.0
Red-Tailed Hawk	*Buteo jamaicensis*	563.0
Northwestern Crow	*Corvus caurinus*	802.9
Sooty Grouse	*Dendragapus fuliginosus*	1055.5
Pileated Woodpecker	*Dryocopus pileatus*	287.5
Mew Gull	*Larus canus*	388.5
Band-Tailed Pigeon	*Patagioenas fasciata*	379.4
Barred Owl	*Strix varia*	716.5
Unidentified Grouse	Subfamily: Tentraoninae	789.5
Average Large Bird	-	802.9
Medium Bird		
Northern Flicker	*Colaptes auratus*	157.4
Steller's Jay	*Cyanocitta stelleri*	128.0
Hairy Woodpecker	*Dryobates villosus*	80.3
Varied Thrush	*Ixoreus naevius*	79.4
Canada Jay	*Perisoreus canadensis*	70.2
Red-Breasted Sapsucker	*Sphyrapicus ruber*	58.2
American Robin	*Turdus migratorius*	79.9
Average Medium Bird	-	93.4
Small Bird		
Swainson's Thrush	*Catharus ustulatus*	29.8

Downy Woodpecker	*Dryobates pubescens*	27.9
Spotted Towhee	*Pipilo maculatus*	41.8
Average Small Bird	-	33.2
Large Mammal		
Mountain Beaver	*Aplodontia rufa*	1005.0
Snowshoe Hare	*Lepus americanus*	1340.0
Average Large Mammal	-	1172.5
Medium Mammal		
Short-Tailed Weasel	*Mustela erminea*	219.0
Bushy-Tailed Woodrat	*Neotoma cinerea*	374.7
Rat	*Rattus* sp.	269.8
Douglas Squirrel	*Tamiasciurus douglasii*	203.5
Red Squirrel	*Tamiasciurus hudsonicus*	224.5
Small Mammal		
Average Medium Mammal	-	258.3
Flying Squirrel	*Glaucomys sabrinus*	155.5
Bat	*Myotis* sp.	5.8
Chipmunk	*Neotamias* sp.	66.4
Shrew	*Sorex* sp.	7.1
Vole	Subfamily: Avicolinae	34.4
Unidentified Items		
Average Small Mammal	-	53.8
Average Large Item	-	987.7
Average Medium Item	-	175.8
Average Small Item	-	43.5

Table 2.2: Summary of prey items recorded at active Northern Goshawk nests in south coast British Columbia in 2019 and 2020 using nest cameras (*n* = 13 sites), pellets (*n* = 25 sites), and prey remains (*n* = 30 sites).

			Camera		Pellets		Remains	
Common name	Scientific name	Total count	% items	% biomass	% items	% biomass	% items	% biomass
Aves								
Northern goshawk	*Accipiter gentilis*	2	-	-	-	-	1.65	1.76
Mallard	*Anas platyrhynchos*	1	-	-	-	-	0.83	1.56
Ruffed grouse	*Bonasa umbellus*	5	0.80	2.06	-	-	0.83	0.72
Great horned owl	*Bubo virginianus*	2	0.40	2.54	-	-	-	-
Red-tailed hawk	*Buteo jamaicensis*	1	0.20	0.63	-	-	-	-
Swainson's thrush	*Catharus ustulatus*	7	1.21	0.20	0.74	0.16	-	-
Northern flicker	*Colaptes auratus*	14	-	-	6.67	7.78	4.13	1.08
Steller's jay	*Cyanocitta stelleri*	18	1.21	0.72	2.96	2.81	6.61	1.31
Sooty grouse	*Dendragapus fuliginosus*	8	0.60	2.97	-	-	4.13	6.50
Downy woodpecker	*Dryobates pubescens*	3	0.60	0.09	-	-	-	-
Hairy woodpecker	*Dryobates villosus*	4	0.40	0.18	1.48	0.88	-	-
Pileated woodpecker	*Dryocopus pileatus*	3	0.20	0.32	-	-	1.65	0.79
Varied thrush	*Ixoreus naevius*	22	2.41	1.03	1.48	0.87	6.61	0.81
Mew gull	*Larus canus*	1	-	-	-	-	0.83	0.53
Band-tailed pigeon	*Patagioenas fasciata*	4	0.60	1.28	-	-	0.83	0.52
Canada jay	*Perisoreus canadensis*	5	1.01	0.39	-	-	-	-
Spotted towhee	*Pipilo maculatus*	3	-	-	1.48	0.46	0.83	0.06
Red-breasted sapsucker	*Sphyrapicus ruber*	5	-	-	1.48	0.64	2.48	0.24

Barred owl	*Strix varia*	2	0.20	0.81	-	-	0.83	0.98
American robin	*Turdus migratorius*	4	0.80	0.31	-	-	-	-
Unknown	-	162	13.68	4.67	25.19	11.14	49.59	56.70
TOTAL BIRDS		**276**	**24.35**	**18.21**	**41.48**	**24.75**	**81.82**	**73.55**
Mammalia								
Mountain beaver	*Aplodontia rufa*	1	0.20	1.13	-	-	-	-
Flying squirrel	*Glaucomys sabrinus*	3	0.60	0.52	-	-	-	-
Snowshoe hare	*Lepus americanus*	17	1.01	7.53	-	-	9.92	22.00
Short-tailed weasel	*Mustela erminea*	1	0.20	0.25	-	-	-	-
Bat	*Myotis* sp.	1	0.20	0.01	-	-	-	-
Chipmunk	*Neotamias* sp.	8	1.41	0.52	0.74	0.36	-	-
Bushy-tailed woodrat	*Neotoma cinerea*	2	0.20	0.42	-	-	0.83	0.51
Rat	*Rattus* sp.	22	4.43	6.67	-	-	-	-
Shrew	*Sorex* sp.	1	0.20	0.01	-	-	-	-
Douglas squirrel	*Tamiasciurus douglasii*	255	39.03	44.38	40.74	60.88	4.96	1.67
Red squirrel	*Tamiasciurus hudsonicus*	10	1.81	2.27	-	-	0.83	0.31
Unknown	-	40	3.02	7.32	17.04	14.01	1.65	1.96
TOTAL MAMMALS		**361**	**52.31**	**71.04**	**58.52**	**75.25**	**18.18**	**26.45**
Unknown								
Unknown	-	116	23.34	10.75	-	-	-	-
GRAND TOTAL		**753**	**100.00**	**100.00**	**100.00**	**100.00**	**100.00**	**100.00**

Table 2.3: Number of prey items recorded at active Northern Goshawk nests in the coastal ecosystem zone and transitional ecosystem zone in south coast British Columbia during 2019 and 2020 using nest cameras (n = 13 sites), pellets (n = 25 sites), and prey remains (n = 30 sites).

			Camera		Pellets		Remains	
Common name	Scientific name	Total count	Coastal	Transition	Coastal	Transition	Coastal	Transition
Aves								
Northern goshawk	*Accipiter gentilis*	2	-	-	-	-	-	2
Mallard	*Anas platyrhynchos*	1	-	-	-	-	1	-
Ruffed grouse	*Bonasa umbellus*	5	-	4	-	-	-	1
Great horned owl	*Bubo virginianus*	2	-	2	-	-	-	-
Red-tailed hawk	*Buteo jamaicensis*	1	-	1	-	-	-	-
Swainson's thrush	*Catharus ustulatus*	7	3	3	-	1	-	-
Northern flicker	*Colaptes auratus*	14	-	-	6	3	4	1
Steller's jay	*Cyanocitta stelleri*	18	2	4	1	3	3	5
Sooty grouse	*Dendragapus fuliginosus*	8	1	2	-	-	2	3
Downy woodpecker	*Dryobates pubescens*	3	-	3	-	-	-	-
Hairy woodpecker	*Dryobates villosus*	4	-	2	1	1	-	-
Pileated woodpecker	*Dryocopus pileatus*	3	-	1	-	-	1	1
Varied thrush	*Ixoreus naevius*	22	1	11	1	1	2	6
Mew gull	*Larus canus*	1	-	-	-	-	1	-
Band-tailed pigeon	*Patagioenas fasciata*	4	-	3	-	-	1	-
Canada jay	*Perisoreus canadensis*	5	-	5	-	-	-	-
Spotted towhee	*Pipilo maculatus*	3	-	-	1	1	-	1
Red-breasted sapsucker	*Sphyrapicus ruber*	5	-	-	2	-	1	2

Barred owl	*Strix varia*	2	-	1	-	-	1	-
American robin	*Turdus migratorius*	4	2	2	-	-	-	-
Unknown	-	162	11	57	22	12	30	30
TOTAL BIRDS		**276**	**20**	**101**	**34**	**22**	**47**	**52**
Mammalia								
Mountain beaver	*Aplodontia rufa*	1	-	1	-	-	-	-
Flying squirrel	*Glaucomys sabrinus*	3	1	2	-	-	-	-
Snowshoe hare	*Lepus americanus*	17	-	5	-	-	1	11
Short-tailed weasel	*Mustela erminea*	1	-	1	-	-	-	-
Bat	*Myotis* sp.	1	-	1	-	-	-	-
Chipmunk	*Neotamias* sp.	8	-	7	-	1	-	-
Bushy-tailed woodrat	*Neotoma cinerea*	2	1	-	-	-	-	1
Rat	*Rattus* sp.	22	1	21	-	-	-	-
Shrew	*Sorex* sp.	1	-	1	-	-	-	-
Douglas squirrel	*Tamiasciurus douglasii*	255	34	160	26	29	-	6
Red squirrel	*Tamiasciurus hudsonicus*	10	-	9	-	-	-	1
Unknown	-	40	2	13	9	14	1	1
TOTAL MAMMALS		**361**	**39**	**221**	**35**	**44**	**2**	**20**
Unknown								
Unknown	-	116	37	79	-	-	-	-
GRAND TOTAL		**753**	**96**	**401**	**69**	**66**	**49**	**72**

Table 2.4: Summary of percent mammalian, avian, and key prey from selected studies of Northern Goshawk diet in North America. Data sources are d (direct observation), r (prey remains), p (pellets), and c (nest cameras). Quantification methods are b (percent of biomass), i (percent of items), m (percent of metabolizable energy), and f (frequency of occurrence).

Study	Location	Ecosystem type	Source	Method	% mammal	% bird	Key prey sp.	% key prey
Schaffer (1998)	central Alberta	aspen forest	d	b	88.60	11.40	*Lepus americanus*	63.97
Younk and Bechard (1994)	northern Nevada	aspen shrubsteppe	d	i	65.00	32.00	*Urocitellus beldingi*	47.00
Doyle and Smith (1994)	Yukon	boreal forest	d, r	b	85.00	-	*Lepus americanus*	56.00
Grzybowski and Eaton (1976)	New York	eastern deciduous forest	p, r	i	39.00	61.00	*Bonasa umbellus*	18.20
Bosakowski and Smith (2006)	New York, New Jersey	eastern deciduous forest	p, r	i	34.00	66.00	*Bonasa umbellus*	25.20
Miller et al. (2014)	south-central Idaho	pine forest, sagebrush	c	b	78.70	18.50	*Urocitellus beldingi*	74.80
Schnell (1958)	eastern California	pine, mixed-conifer forest	d	b	46.00	54.00	*Cyanocitta stelleri*	23.10
Reynolds and Meslow (1984)	eastern Oregon	pine, mixed-conifer forest	p, r	i	45.00	55.00	-	-
Kennedy (1991)	New Mexico	pine, mixed-conifer forest	d	i	67.00	33.00	*Sciurus aberti*	30.60
	New Mexico	pine, mixed-conifer forest	p	i	49.00	51.00	*Sciurus aberti*	41.30
	New Mexico	pine, mixed-conifer forest	r	i	48.00	52.00	*Sylvilagus* spp.	20.00
Boal and Mannan (1994)	Arizona	pine, mixed-conifer forest	d	b	94.00	6.00	*Sylvilagus* spp.	26.10
Reynolds et al. (1994)	Arizona	pine, mixed-conifer forest	p, r	i	62.00	38.00	*Sylvilagus* spp.	18.00
Watson et al. (1998)	eastern Washington	pine, mixed-conifer forest	p, r	b	53.80	46.20	*Lepus americanus*	40.60
McCoy (1999)	northern California	pine, mixed-conifer forest	d	m	76.00	24.00	*Spermophilus lateralis*	30.00
Rogers et al. (2006)	Arizona	pine, mixed-conifer forest	c	b	88.69	6.92	*Sylvilagus floridanus*	42.31
Smithers et al. (2005)	Minnesota	pine, mixed-hardwood forest	c	i	62.00	38.00	*Tamiasciurus hudsonicus*	31.00
Watson et al. (1998)	western Washington	temperate rainforest	p, r	b	47.10	52.60	Grouse (subfamily Tetraoninae)	43.20
Ethier (1999)	Vancouver Island	temperate rainforest	p	f	-	-	*Tamiasciurus hudsonicus*	69.00
Thrailkill et al. (2000)	western Oregon	temperate rainforest	r	i	16.00	84.00	*Bonasa umbellus*	45.00
Lewis et al. (2006)	southeast Alaska	temperate rainforest	c	i	-	72.80	*Dendragapus obscurus*	21.00
	southeast Alaska	temperate rainforest	c	i	-	90.60	*Falcipennis canadensis*	18.00
Case (2021)	south coast BC	temperate rainforest	c	b	71.00	18.00	*Tamiasciurus* spp.	47.00
	south coast BC	temperate rainforest	p	b	75.00	25.00	*Tamiasciurus* spp.	61.00
	south coast BC	temperate rainforest	p, r	b	36.00	64.00	Grouse (subfamily Tetraoninae)	36.00

Chapter 3

General Conclusion

3.1 Overview

Specialist and generalist predators differ in their degree of dependence on prey species, with cascading consequences for many aspects of their life history (Korpimäki and Norrdahl 1991, Resano-Mayor et al. 2016). Specialist predators are efficient hunters of their main prey at the cost of poor success when hunting other species, whereas generalist predators hunt many species with equal skill (Terraube et al. 2011) and readily switch between alternate prey (Steenhof and Kochert 1988, Terraube and Arroyo 2011). As a result, specialist predators depend on a single species and their demographic parameters–such as migration, reproductive success, and survival–and population density vary in synchrony with its abundance (Korpimäki and Norrdahl 1991, Terraube et al. 2011). In contrast, generalist predators make use of many prey species and their populations are relatively stable (Andersson and Erlinge 1977, Hanski et al. 1991).

The familiar dichotomy between specialist and generalist predators is, of course, an oversimplification. The abundance of a single prey species can be a major driver of demographic parameters for generalist and specialist predators alike (Elmhagen et al. 2000, Resano-Mayor et al. 2016). Furthermore, within a single species some populations (Salamolard et al. 2000, Roth et al. 2007), or some individuals within a population (Woo et al. 2008), may be more or less specialized. A single individual may also become a more specialized hunter over its lifetime as a result of age and experience (Rutz 2006). Correctly identifying the degree of specialization and understanding its effect on demographic parameters is more than a matter of theory or curiosity: the consequences of specialization can scale up from individuals through populations to entire species, with profound implications for conservation (Ferrer and Negro 2004, Terraube et al. 2011, Resano-Mayor et al. 2016).

The complex relationship between dietary specialization and conservation is exemplified by the northern spotted owl (*Strix occidentalis caurina*). Spotted owls depend on old-growth forests, but the cause of this association has been a source of speculation since the early years of spotted owl research (Gutiérrez and Carey 1985). The spotted owl's reliance on old-growth forest appears to be driven, in part, by its relatively specialized diet (Carey et al. 1992, Ward et al. 1998). More than half the biomass spotted owls consume comes from just two taxa, flying squirrels (*Glaucomys sabrinus*) and woodrats (bushy-tailed woodrat *Neotoma cinerea* and dusky-footed woodrat *N. fuscipes*; Smith 1963, Ward et al. 1998, Forsman et al. 2001, 2004). The dominance of flying squirrels and woodrats in the diet holds true across the subspecies' range, although the relative contribution of each taxa varies with geographic region and forest type in response to local abundance. In Washington's Olympic Peninsula, where woodrats are absent, spotted owls consume primarily flying squirrels (Carey et al. 1992), whereas in northern California flying squirrels make up a smaller portion of the diet and woodrats, which are more abundant, dominate (Ward et al. 1998). Even within a single spotted owl population some individuals specialize on one taxa or the other (Zabel et al. 1995). Home range sizes in the flying squirrel-dependent Olympic Peninsula are among the largest ever recorded (Carey et al. 1992), and where both taxa are present owls which consume primarily flying squirrels have larger home ranges than those which consume mostly woodrats (Zabel et al. 1995). Evidently diet and prey abundance affect some demographic parameters, such as breeding density, which has led some authors to recommend increasing prey abundance as a route to increase owl abundance (Forsman et al. 2004). Yet prey abundance alone does not appear to affect spotted owl productivity (Rosenberg et al. 2003). Instead, productivity appears to result from complex interactions between climate and prey abundance (Glenn et al. 2011).

In contrast to the spotted owl's dependence on a few prey species, the northern goshawk is considered a generalist predator and consumes an enormous diversity of prey across its wide geographic range (reviewed in Drennan 2006, Rutz et al. 2006). I identified 29 different prey species in the diet of goshawks in coastal British Columbia, which is consistent with a generalist foraging strategy. However, nearly half of goshawk diet in my study area was composed of *Tamiasciurus* spp. (hereafter "pine squirrels"), which indicates a

level of specialization similar to that of the spotted owl. Some goshawk populations appear to be strongly generalist (e.g. Arizona: Salafsky et al. 2007), whereas in others a key prey species is a major driver of productivity, survival, and other demographic parameters (e.g. Yukon: Doyle and Smith 1994, and Finland: Tornberg et al. 2005). I did not find an effect of the degree of dietary specialization on goshawk productivity. There are several explanations for this unexpected finding. First, specialists may not be more productive than generalists (Woo et al. 2008). Specialist individuals may selectively consume pine squirrels but have similar levels of fitness as generalist individuals in this population. Alternately, specialization may not be the result of selection. Individuals may lack strong prey preferences and take pine squirrels in proportion to their abundance. Total prey abundance, rather than pine squirrel abundance, may then drive productivity (Penteriani et al. 2002). Finally, as in the spotted owl, prey abundance and diet during the breeding season may be a lesser driver of productivity than other factors, such as weather or winter prey abundance.

Goshawk diet varies across its range in response to the regional presence and abundance of specific prey species (Drennan 2006). I found the key prey of goshawks in the south coast region to be pine squirrels. This contrasts with studies of goshawk diet elsewhere in the Pacific Northwest, where the key prey is generally grouse (Watson et al. 1998, Thrailkill et al. 2000, Bloxton 2002, Lewis et al. 2006), but is similar to work on Vancouver Island, where the key prey is also pine squirrels (Ethier 1999). My results also contrast with studies from other regions of western North America, where the key prey may occasionally be a species of squirrel but is most often a species of hare or rabbit. The unexpected difference between diet in my study area and the larger Pacific Northwest may be due in part to differences in methodology. When the results from studies across temperate rainforest ecosystems are standardized (data from pooled pellets-and-remains or remains only, measured by counts), the contrast between regions within the Pacific Northwest is much less pronounced. However, the proportion of mammalian prey in the diet, particularly pine squirrels, remains markedly higher within coastal British Columbia than outside it even after accounting for methodological differences. The relatively high specialization on pine squirrels may be a result of higher pine squirrel abundance compared to other temperate rainforest ecosystems (Carey 1995, Ransome and Sullivan 2003). No Pacific Northwest

study has assessed goshawk diet and absolute prey abundance simultaneously (though see Ethier 1999). Nonetheless, regional data hint at a pattern of higher dietary specialization in areas or forest types with higher pine squirrel abundance (see Fig. 3.1). Across the two ecological zones present in my study area I observed only minor variation in goshawk diet and no variation in the dominance of pine squirrels in the diet. If goshawks are more specialized on pine squirrels in areas where pine squirrels are more abundant, this indicates a slight difference in the prey community of these two zones but a similar abundance of pine squirrels. The wide variety of prey species consumed, combined with the consistent specialization on pine squirrels despite variation in prey community, suggests goshawks in my study are generalist predators opportunistically exploiting a locally abundance prey species.

3.2 Directions for Future Research

Comparing the foraging ecology of the northern spotted owl and the northern goshawk highlights significant knowledge gaps regarding goshawk biology. The controversy surrounding spotted owl conservation, combined with its position at the heart of a major management plan, has made it one of the most-studied birds in the world (Gutiérrez et al. 2020). The northern goshawk, although likewise shrouded in controversy, has not received the same level of study. Where data are available, it is more difficult to generalize research on the widespread, generalist northern goshawk than for the more restricted, relatively specialized spotted owl. As a result, there is a pressing need for detailed, local information on goshawks in the Pacific Northwest, particularly in coastal British Columbia.

One knowledge gap related to the work I present here is how variation in prey abundance affects the degree of dietary specialization, productivity, and survival of individual goshawks. Dietary specialization such as goshawks in my study area exhibit may be the result of a preference for the main prey or simply an absence of other options. Data on prey abundance is necessary to understand the mechanism of goshawk specialization and whether it is the result of high selectivity for pine squirrels, high abundance of pine squirrels, or some combination of both. This information can in turn be used to evaluate how changes in key prey abundance and total prey abundance influence goshawk demographic parameters, particularly productivity. Without this knowledge it is impossible

to fully understand the factors limiting goshawk populations in coastal British Columbia.

A second knowledge gap is how the amount and type of habitat goshawks use for foraging varies with diet and prey abundance. Goshawk home range size varies across their geographic range and goshawks have been observed foraging in diverse habitat types, leading to ongoing debate over how and why goshawks select habitat (Greenwald et al. 2005, Reynolds et al. 2008). Research on spotted owls indicates that home range size is inversely related to prey abundance and foraging habitat selection varies with the identity of the main prey (Zabel et al. 1995). Variation in goshawk home range size and habitat selection may likewise be explained by diet and prey abundance (Kenward 1982, Penteriani et al. 2013). If so, foraging habitat management could only be conducted with knowledge of goshawk diet, and recommendations made for one population could be applied to others only with great caution. Filling this knowledge gap with information specific to coastal British Columbia is vital and has been identified as a priority by goshawk managers (NGRT 2008, Parks Canada Agency 2018).

To address the crucial foraging habitat knowledge gap, the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development (FLNRORD) and I conducted a pilot study of foraging habitat use in coastal British Columbia. Between 2018-2020 we tagged and tracked 4 male and 9 female goshawks. Captures were conducted during the early breeding season using a dho-gaza trap with a live great-horned owl (*Bubo virginianus*) as a lure (Bloom et al. 2007). Goshawks were fitted with 14-gram solar-powered GPS-UHF tags (Ecotone Telmetry brand, Harrier model) with an additional VHF tag, attached via backpack-style harness. Tags were programmed to take a location point every 15 minutes and to download data to a base station when within range (approximately 100 m from the station). Base stations were placed beneath or above nests and tags were program to check for proximity to the station every 15 minutes.

We were able to retrieve data from 10 out of 13 birds, collecting location data from 3 - 73 (mean = 37.9 $\pm$ 26.7 standard deviation) days of the breeding season (20 April - 15 September; Table 3.1). Tracked birds provided 45 - 2964 location points ($\bar{x}$ = 837.78 $\pm$ 923) with an average of 31.03 ($\pm$ 62.28) locations per bird per day. Over the study period we

observed only one probable mortality. I estimated breeding season home ranges and core-use areas using 95% minimum convex polygons (MCPs) and 50% MCPs, respectively. The mean breeding season home range was 2008.9 ha, but male home ranges were far larger than female home ranges (male $\bar{x}$ = 4409.2 $\pm$ 1408.4, *n* = 4; female $\bar{x}$ = 88.7 $\pm$ 115.8, *n* = 5; *t* = -6.12, df = 3.03, *P* = 0.01). Male core-use areas were also larger than female core-use areas, but not significantly so (male $\bar{x}$ = 851.5 $\pm$ 508.3; female $\bar{x}$ = 1.3 $\pm$ 2.3; *t* = -3.35, df = 3, *P* = 0.04). Female home ranges and core-use areas were smaller due to the significantly higher amount of time females spent within approximately 100 meters of the nest (*t* = -3.32, df = 6.9, *P* = 0.01). Males also traveled further from the nest than females. The average furthest distance from the nest a male traveled was 7.05 ($\pm$ 1.76) km, while on average females only ventured 2.86 ($\pm$ 2.02) km from the nest (*t* = -3.32, df = 6.9, *P* = 0.01). Home ranges were rarely circular, but rather shaped by geographic constraints such as coastlines or mountains peaks (see Fig. 3.2). Within home ranges, kernel density estimates show habitat use is not even across a male's territory. Instead, there are clusters of activity around areas which are likely high-quality foraging habitat.

We encountered several challenges over the course of the three-year pilot. First, the location data we obtained were biased toward females. Females are more aggressive near the nest than males and so are more likely to be captured when using the dho-gaza trapping method. Data from female tags downloaded more frequently onto the base stations than data from male tags because of the large amount of time females spent near the nest, where the base stations were located. Consequently, we collected far more location data on females than males, which offered relatively little insight into foraging habitat use since males provide most of the food during the breeding season. Second, we were unable to retrieve data from some tagged birds. Several birds were detected via the VHF transmitter but could not be relocated with sufficient precision to download data from the UHF tag. As a result, we could not retrieve data from the winter or subsequent breeding season. Our inability to relocate birds is likely due to a combination of the limited range of the VHF tags and the difficult topography of our study area, compounded by the birds' failure to return to known breeding areas. Finally, technical malfunctions resulted in no data downloads for two birds, too many location points for one birds, and too few location points for several others. Future work should consider more powerful VHF tags

for easier relocation and an alternate-days duty cycle to increase battery life and reduce the number of missed locations.

Despite these setbacks, the pilot study provided insight into goshawk movement and habitat use, with relevance to goshawk management. The GPS data we were able to retrieve, although less than anticipated, was of higher resolution than VHF data and higher accuracy than satellite data. It may therefore be uniquely well-suited to studies of foraging habitat selection. Our average breeding season home-range for males are slightly larger than most reported elsewhere in North America, but our average female home range in much smaller (Table 3.2). The high fidelity of females to the nest area confirms the importance of protected buffers around nests to prevent the disturbance of habitat critical for breeding females and fledglings. However, the large distances traveled by males and the irregular shape of their home ranges shows that circular buffers based on estimates of mean home range size are not good approximations of true space use. Areas used extensively by males usually fall outside the nest area and are not be captured by current nesting habitat protections. Preliminary inspection of movement data indicates goshawks readily crossed narrow barriers such as roads, rivers, and powerline cuts, and sometimes appeared to use these features for travel or foraging. On the other hand, goshawks seemed to generally route around larger barriers such as lakes or clearcuts. This suggests managed areas around nests should be tailored to the amount and configuration of suitable foraging habitat present in the surrounding landscape, and that any timber harvest within the foraging area should prioritize the preservation of connectivity between patches of high-quality foraging habitat. However, a great deal of additional research is needed to confirm and refine these suggestions, particularly regarding the characteristics of suitable and high-quality foraging habitat.

3.3 Management Implications of Goshawk Diet

Climate change is one of the largest and most difficult to anticipate threats facing biodiversity (Bellard et al. 2012). The current understanding of how climate change will impact goshawks in coastal British Columbia is largely speculative (Parks Canada Agency 2018). Although I found no evidence of a link between the degree of dietary specialization and goshawk productivity, the level of specialization I observed and findings from other

studies suggest goshawks in my study area are highly dependent on pine squirrels for successful reproduction. Notably, Ethier (1999) found goshawk productivity on Vancouver Island to be significantly correlated with red squirrel abundance. Pine squirrels are themselves highly dependent on conifer seeds and their abundance varies with the size of the annual cone crop (Smith 1970). Seed production is cyclical but may be promoted by higher temperatures and inhibited by drought (Boucher et al. 2020). As the climate warms and drought risk rises, climate-driven changes in seed production may cascade through prey abundance to impact goshawk populations in coastal British Columbia. Significantly more work is needed to understand the relationship between prey abundance, the buffering ability of alternate prey, and goshawk productivity, but my results provide an important starting point for incorporating climate change into goshawk management.

Wildlife management, whether founded on a single-species or ecosystem-based approach, generally centers around species, subspecies, or unique populations at risk of extinction. My thesis examines a single population of goshawks on the south coast of British Columbia which is currently classified as part of the subspecies *laingi*. The precise range of *laingi* has never been entirely clear, but recent genetic evidence indicates the Haida Gwaii population is highly unique and distinct from other putative *laingi* populations (Geraldes et al. 2018). My results suggest a strong ecological similarity between goshawks within my study area, Vancouver Island, and Haida Gwaii, where goshawks are also highly dependent on pine squirrels (COSEWIC 2013). The diet of these populations stands in contrast to others in temperate rainforest ecosystems which are currently considered *laingi*, such as the Olympic Peninsula or Southeast Alaska, where goshawks consume mainly birds. Goshawks in coastal British Columbia may therefore be ecologically similar to each other, and ecologically distinct from other populations, regardless of their genetic relationship. The ecological similarity of these populations supports the strategy used by the Northern Goshawk Recovery Team to delineate the boundaries of the *laingi* range, which emphasizes ecosystem mapping over genetics (NGRT 2008).

Rooting management in ecosystems, rather than individual species, has been a success–albeit a conditional one–for forest conservation in the United States. Ecosystem-based management has also been applied in the temperate rainforests of

British Columbia. In the early 2000s an ecosystem-based management plan, which includes the northern goshawk as a focal species, was developed for the Great Bear Rainforest on the northern coast of British Columbia (Price et al. 2009). My work provides some of the habitat-specific ecological information needed to broaden existing single-species goshawk management, or even to incorporate goshawks as a focal species in future ecosystem-based management. While it will be years before the success of Great Bear Rainforest agreement can be assessed, the groundbreaking plan offers a glimpse of the future of forest management in British Columbia–and the role northern goshawks may play in it.

3.4 Figures and Tables

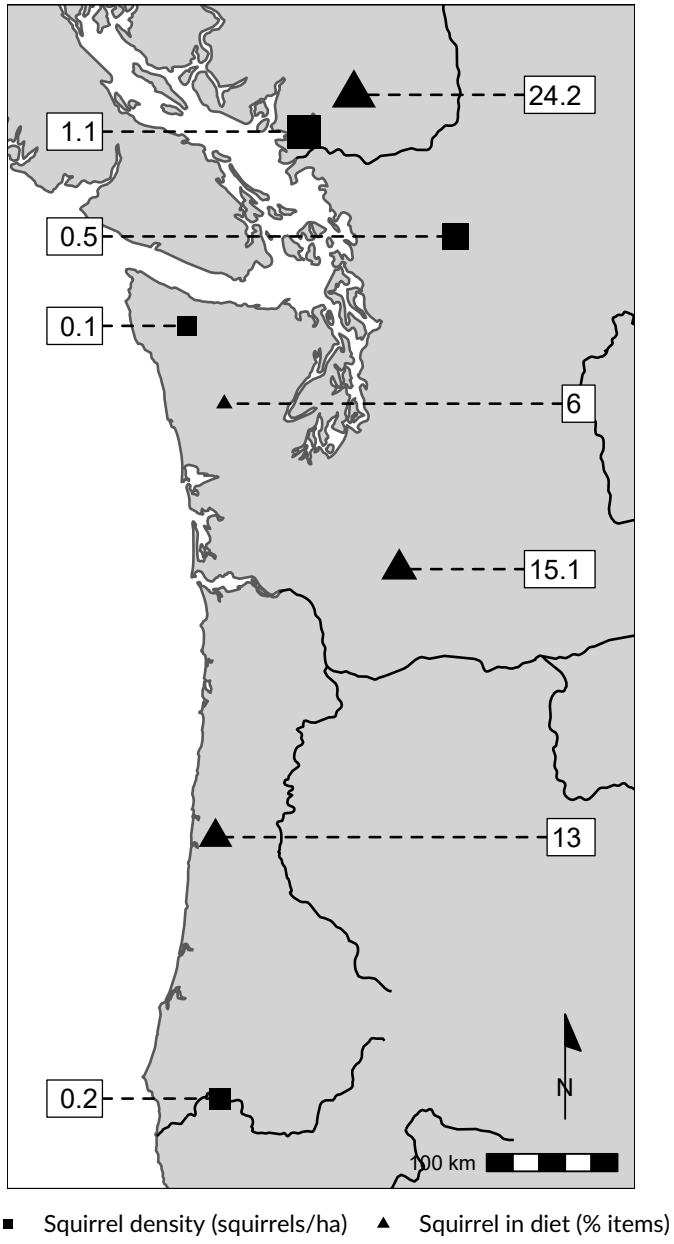

Figure 3.1: Northern Goshawk dietary specialization and pine squirrel (*Tamiasciurus* spp.) density in the Pacific Northwest. Dietary specialization (percent of prey items) estimated using pooled pellets-and-remains (Watson et al. 1998, Bloxton 2002, this study) or remains only (Thrailikill et al. 2000). Pine squirrel density (individuals per ha) estimated by mark-recapture (Carey et al. 1992, Ransome and Sullivan 2003). Symbol location indicated approximate study location and size represents relative degree of specialization or density.

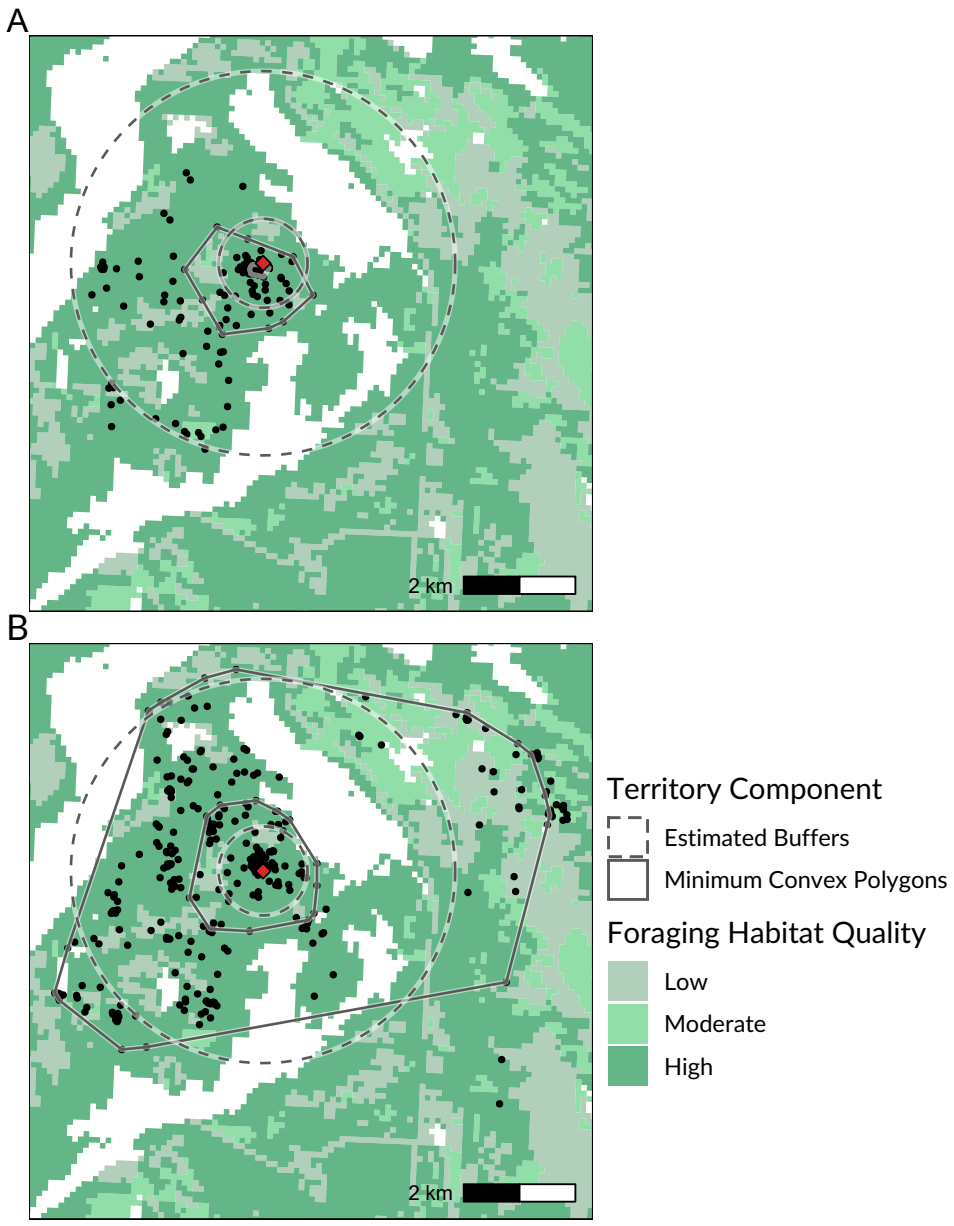

Figure 3.2: Representative examples of breeding season home range and core-use area of one female (A) and one male (B) goshawk tagged at the same site (red diamond) in 2019 and 2020, respectively. Habitat quality from habitat suitability model (Mahon 2008) show in green, with water in white. Breeding season home range and core-use areas estimated using 95% and 50% MCPs, shown with solid lines. Estimated home range (3450 ha) and breeding area (200 ha) buffers used in goshawk management (NGRT 2008, Parks Canada Agency 2018) are shown with dashed lines. Individual location points shown as black circles.

Table 3.1: Summary of data from pilot telemetry study on Northern Goshawk in south coast British Columbia using GPS-UHF tags. Describes location data, maximum distance recorded from nest, percentage of points within 100 m of nest, and breeding season home range size (50% and 95% minimum convex polygons and kernel density estimates.

		Location data				Relation to nest		Home range (ha)			
ID	Site	First point	Last point	N. days	N. points	Max. distance	% at nest	50% MCP	95% MCP	50% KDE	95% KDE
Female											
HAR10	MTC	2019-05-02	2019-06-29	58	315	5457	78.4	0.3	58.9	8.7	113.4
HAR08	TCR	2019-06-10	2019-06-27	17	45	76	82.2	0.0	0.2	0.0	0.4
HAR03	GRV	2020-06-08	2020-06-28	20	2964	2441	95.9	0.0	0.0	0.0	0.0
HAR02	RLK	2020-06-13	2020-07-08	25	977	4013	72.1	5.4	280.6	12.7	267.4
HAR12	FMT	2020-06-25	2020-06-28	3	104	2302	3.9	0.7	103.7	13.0	152.1
AVERAGE				**25**	**881**	**2858**	**66.5**	**1.3**	**88.7**	**6.9**	**106.7**
Male											
HAR07	TCR	2018-07-08	2018-09-14	68	637	7977	0.0	904.8	4531.4	850.6	5263.1
HAR09	MTC	2019-05-02	2019-07-02	61	409	4413	2.4	530.1	2611.2	636.3	3032.8
HAR04	RLK	2019-06-22	2019-07-08	16	532	7773	9.0	423.0	4441.1	662.3	4407.6
HAR05	SKA	2019-06-23	2019-09-04	73	1557	8026	0.0	1548.2	6052.9	1642.2	6674.7
AVERAGE				**54**	**784**	**7047**	**2.9**	**851.5**	**4409.2**	**947.9**	**4844.5**

Table 3.2: Summary of Northern Goshawk breeding season home range size (sample size) in ha estimated by 95% minimum convex polygons (MCP) or kernel density methods (KDE) from selected studies in North America. Methods are v (VHF transmitter), g (GPS logger), or s (satellite transmitter), and mcp (minimum convex polygon) or kde (kernel density).

				Home range (ha)		
Study	Location	Ecosystem Type	Method	Comb.	Female	Male
Doyle and Smith (1994)	Yukon	boreal forest	v, mcp		2880 (1)	4000 (1)
Moser and Garton (2019)	northern Idaho	mixed conifer forest	s, kde		3859 (12)	5146 (7)
Hasselbad and Bechard (2007)	south-central Idaho	pine and aspen forest, sage shrubsteppe	v, mcp			790 (6)
Hargis et al. (1994)	eastern California	pine forest	v, kde		1340 (7)	2400 (2)
Austin (1993)	southern Oregon	pine, mixed-conifer forest	v, mcp		3774[a] (5)	2425[a] (5)
Blakey et al. (2020)	northern California	pine, mixed-conifer forest	g, kde		1619 (12)	3926 (8)
Bright-Smith and Mannan (1994)	northern Arizona	pine, mixed-conifer forest	v, mcp			1758 (11)
Sonsthagen et al. (2006)	Utah	pine, mixed-conifer forest	s, kde		10140[b]-17650[c] (16)	
Boal et al. (2003)	northern Minnesota	pine, mixed-deciduous forest	v, mcp		2495 (11)	2593 (17)
Bloxton (2002)	Western Washington	temperate rainforest	v, kde	3516 (12)		
Case (2021)	south coast British Columbia	temperate rainforest	g, mcp		88.7 (5)	4409.2 (4)
Titus et al. (1996)	southeast Alaska	temperate rainforest	v, mcp		19215[d] (8)	5847 (8)

[a] 100% MCP
[b] Residents
[c] Migrants
[d] Several females tagged late in season or abandoned nest

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